ations (spurious or otherwise) in the presence of the illuminated disk. If adventitious reward were effective during the differential condition, surely it would continue to be effective in sustaining a high rate of pecking in the nondifferential condition as well.

As a further check on the importance of the differential association of disk illumination with feeding, we studied five new birds on the nondifferential condition. After 14 days of nondifferential exposure to grain presentation, a total of ten pecks had been recorded for all five birds together. All of these occurred during the intertrial interval when the key was not illuminated. Apparently, the decline in responding seen in the first experiment was not an artifact of changing the procedures, nor was it related to prior exposure to a difference in reinforcement density. Acquisition, as well as maintenance of pecking, is dependent on a differential association of key and reinforcer.

When these new birds were shifted to the original differential procedure, all eventually began pecking the disk. Even after 35 days of exposure, however, the mean rate of response was only 20 per minute, and there was no overlap between the rates of pecking of these birds and those of the first group, whose mean terminal rate was 101 responses per minute. Thus, there was a residual effect of nondifferential reinforcement, even after successful acquisition had taken place.

These results demonstrate three important aspects of the autoshaping phenomenon, all of which are consistent with the assumption that classical conditioning is a fundamental factor in the phenomenon. First, we have shown that a specific signaling relationship is not important for acquisition or sustained maintenance of behavior. Second, the necessity for differential pairing in maintenance, as well as acquisition, indicates that informational properties of a stimulus, rather than its mere association with feeding, are responsible for the phenomenon. Third, the phenomenon, although obviously susceptible to analysis by principles of classical conditioning, offers little basis for an account in terms of adventitious reinforcement.

The pecking engendered by autoshaping is directed to a significant part of the environment—that is, a part correlated with the opportunity to eat. The strong and direct control over behavior

exerted by stimulation of a mechanism in pigeons is much like that exerted in new environments by the process by which organisms tailor their controlled without the involvement of reward and punishment. The findings of the Brelands (5) in a number of nonavian species suggest that such mechanisms are not peculiar to pigeons. Although study of the way in which complex activities are developed and learned has largely excluded effects other than those of reward and punishment, it now seems necessary to include some other factors as well, if the principles of adaptive learning are to provide an adequate account of the development and maintenance of effective but often nonarbitrary behavior. It is apparent that animals do not select behaviors randomly from their repertoire in new situations. The manifestation of associative learning that we have ex-

prior to any "shaping" effect by reward and punishments.

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Echolocation in Bats: Signal Processing of Echoes for Target Range

Abstract. Echolocating bats Eptesicus fuscus and Phyllostomus hastatus can discriminate between the nearer and farther of two targets. Their errors in discrimination are predicted accurately by the autocorrelation functions of their sonar cries. These bats behave as though they have an ideal sonar system which cross correlates the transmitted cry with the returning echo to extract target-range information.

Bats of the suborder Microchiroptera use a type of active sonar for orientation (1). Biologists, psychologists, and physicists have speculated often about the kinds of information available to the bat from echoes and about the nature of the mechanism which processes the echoes from targets in the bat's environment. The possibility of depth perception or target ranging by echolocation has received particular attention (2–5). The ease with which bats detect and avoid obstacles and detect, track, and capture airborne targets seems to require some means of determining the distance to targets (6).

Three specimens of the North American insectivorous bat, Eptesicus fuscus, and three specimens of the neotropical, carnivorous and frugivorous bat, Phyllostomus hastatus, learned to discriminate target range in the experiment reported here. The bats were blinded (enucleated) several months prior to the experiment to eliminate the possible use of vision, since the experiment could not be conducted in darkness. Each bat learned to fly from a

small, elevated platform to the closer of two other platforms (Fig. 1). A triangular target 10.0 cm wide and 5.0 cm high was mounted at the back of each of the two landing platforms. The platforms were separated by an angle of 40° when viewed from the bat's position on the starting platform.

The landing platforms differed from each other in the distance from the bat on the starting platform to the target. The bat learned to fly to the nearer platform in a straightforward simultaneous discrimination procedure with food as reward (a piece of a mealworm offered in forceps) and without correction of error trials. To make training easier, each bat was deprived of some of its normal food intake until it reached 90 to 95 percent of its weight when captured. The closer platform alternated left to right according to a pseudo-random schedule (7).

At first the nearer target appeared at a distance of 50 cm. The farther target was 60 cm from the bat throughout the experiment. After the bat reached a criterion of better

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Fig. 1. The apparatus for target-range discrimination by echolocating bats, showing the starting platform and the two landing platforms with the targets.

than 95 percent correct responding for three consecutive days at 25 trials per day, the nearer target was presented in a series of new positions, a new one every other day. The bat responded for 50 trials on each position of the nearer target. Changes were preceded by five warm-up trials at the position of the previous day. The nearer target appeared at 51 cm, then 52 cm, then 53 cm, and so forth until both targets appeared at the same distance, 60 cm. On succeeding days the difference in target range was 10, 9, 8, 7, 6, 5, 4, 3, 2, 1.5, 1, 0.5, and finally 0 cm. After the trials on each of the last four differences in the series, the bat was tested at a difference of 3 cm to determine whether exposure to difficult discriminations had impaired the bat's responding.

The bats readily learned the flying response, reached the initial criterion, and proceeded through the discrimination series without difficulty. None of the bats suffered in performance on the 3-cm difference after the trials on more difficult discriminations. During each trial, the bat scanned both targets with its sonar and then flew directly to the left or the right platform.

Eptesicus can discriminate a range difference of about 13 mm 75 percent correctly, and *Phyllostomus* can discriminate 12 mm (Figs. 2 and 3). At an absolute distance of 60 cm, these two species have an acuity of about 2 percent in discriminating target range. The choice of 75 percent correct is an arbitrary criterion for discrimination.

Condenser microphones were mounted on the landing platforms and on the starting platform to monitor the bat's scanning during each trial and to obtain good recordings of the cries for analysis. *Eptesicus* emitted 1.0- to 2.5-msec cries with a peak sound pressure of about 50 to 100 dyne/cm^2.

The cries were frequency-modulated (FM) and swept from about 50 khz to about 25 khz with very little second harmonic energy present. *Phyllostomus* used 0.5- to 1.0-msec cries with an amplitude of 2 to 15 dyne/cm^2. These cries were also FM with harmonically related sweeps covering a range of frequencies from around 65 to about 30 khz. The echoes returned to *Eptesicus* by the target at 60 cm were in the vicinity of 0.3 dyne/cm^2. The echoes for *Phyllostomus* were near 0.05 dyne/cm^2. They were certainly audible to the bats (8, 9). Since the bats were without vision, the discriminations were mediated by sonar.

The nearer target subtended a larger angle in the bat's sonar field, and it produced a slightly stronger echo than the farther target due to the smaller attenuation factor for a shorter air path traveled by the echo. Although such artifacts might be discriminable to the bat for range differences of several centimeters or more, it seems unlikely that they would be useful for a range difference of only 12 to 13 mm. The minimum discriminable size difference for targets similar to those used here is 17 percent of the area of the larger triangle for *Eptesicus* (10). Such a size difference would require a range difference of over 30 mm, so it does not appear that the "apparent size" difference between the nearer and farther targets influenced the data on distance discrimination.

The difference in arrival time of echoes from the nearer and farther targets probably carried the information about target range. The outgoing and returning time difference is 70 to 75 μsec for range differences of 12 to 13 mm.

All of the information potentially available in a returning echo about echo arrival time, and hence target range, is contained in the cross-correlation function of the transmitted and received sonar signals (11–13). The inputs to a sonar receiver are signals separated by some difference in arrival time associated with the target's range. The input also includes noise. In the laboratory the ambient noise in the bat's frequency band was below the measuring limits of the available equipment, so the environmental signal-to-noise ratios for the echoes reflected back to *Eptesicus* and *Phyllostomus* exceeded +30 to +40 db. Under such favorable noise conditions the
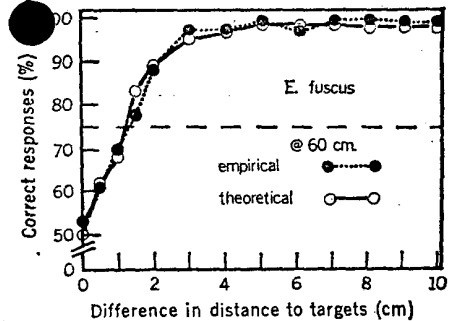
Fig. 2. The average performance of three *Eptesicus* in discriminating differences of target range (empirical curve), and the performance predicted from the autocorrelation function of the *Eptesicus* sonar cry (theoretical curve).

output of an ideal sonar receiver is essentially the cross-correlation function of the input signals (13). In practical situations the envelope of the cross-correlation function is usually taken to represent the ambiguity encountered by an ideal receiver in estimating target range from the signals appearing at the input (12, 13). In the absence of target motion and consequent Doppler shift of the echo, the autocorrelation function of the sonar transmission is a satisfactory approximation of the desired cross-correlation function (12).

Autocorrelation functions for the cries of *Eptesicus* and *Phyllostomus* were derived from the recordings made during discrimination trials (14). Assume that the rate at which the bat makes errors in judging target distance or echo arrival time is more or less directly related, for any given time separation, to the magnitude of correlation between signals as represented by the envelope of the autocorrelation
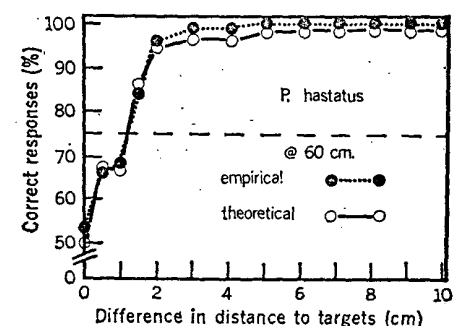

Fig. 3. The average performance of three *Phyllostomus* in discriminating differences of target range (empirical curve), and the performance predicted from the autocorrelation function of the *Phyllostomus* sonar cry (theoretical curve).

function (Fig. 4). High correlation would lead to poor discrimination, and low correlation would result in good discrimination. At zero time separation, when correlation is highest and there is in fact no difference in target range to be discriminated, the bat would be unable to perform beyond chance levels (50 percent correct responses).

The "theoretical" curves in Figs. 2 and 3 show the distance discriminations that would be predicted from the envelopes of the autocorrelation functions of the cries of *Eptesicus* and *Phyllostomus* if one assumes a rough correspondence between signal correlation and number of errors made by the bat (*15*). Both *Eptesicus* and *Phyllostomus* perform as though they used ideal sonar systems operating on the echoes of their respective cries with a cross-correlation receiver.

It has been proposed that bats derive target information from the envelopes of the outgoing cries and returning echoes or from a perceived pitch associated with the time interval separating trains of cries and echoes (*5*). In such cases much of the information carried in the waveforms of the individual signals would be discarded. The results of the distance-discrimination experiment indicate that most of the information in the signals is actually preserved and processed by the bat, and that target ranging is dependent upon the detailed frequency structure of the echo rather than upon echo envelopes or trains of cries and echoes. Electrophysiological observations on evoked potentials and single-unit responses in the bat's auditory system establish that precise analysis of individual echo signals is possible (*2, 3, 9, 16*).

One form of cross-correlation processing, pulse compression, has been suggested for target ranging by bats (*4*). The basilar membrane of the bat's cochlea does not, however, act as a dispersive delay line in a manner suitable for pulse compression (*4, 11*). Cross correlation of transmitted and received signals may take place at some point in the bat's auditory brain without requiring a delay line at the cochlea serving as a filter matched to the bat's cries (*2, 3, 9, 11, 16*).

The most probable location for the neural cross correlator is in the inferior colliculus, an auditory center much enlarged in the bat's brain. The acuity of obstacle avoidance by echolocation in *Myotis* is relatively unaffected by
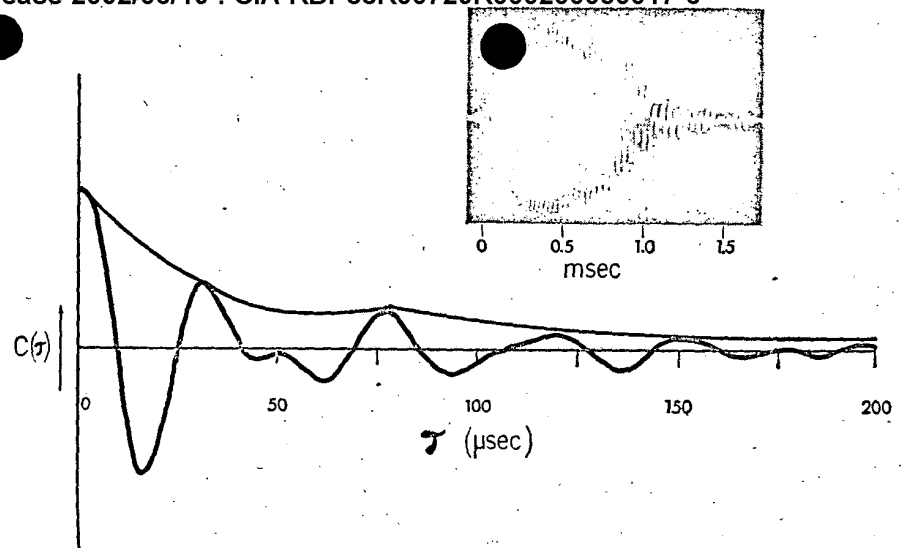
Fig. 4. The autocorrelation function of an *Eptesicus* sonar cry for time-delay differences up to 200 μsec, showing the upper envelope of the function. (Inset) The oscilloscope trace of the cry itself. The envelope of the autocorrelation function represents the ambiguity in echo arrival time (target range) confronting the bat when it processes the echoes of its cries.

bilateral ablation of the auditory cortex or by unilateral damage to the inferior colliculus, whereas bilateral ablation of the ventral portion of the inferior colliculus severely impairs echolocation (*17*). Single units in the cochlear nucleus show little of the sophistication of units in the inferior colliculus for the analysis of bat-like, FM signals. The response properties of neurons in the inferior colliculus suggest that these units function as a neural "template" mechanism for the processing of cries and echoes (*3, 9, 16*).

The target-ranging performance reported here is direct behavioral evidence that the bat processes individual echo signals in detail for the arrival-time information they contain. Apparently the bat possesses a sonar receiver with ideal properties. The bat effectively stores the outgoing sonar signal in the main nucleus of the inferior colliculus. The storage mechanism probably involves the complex response characteristics of neurons in the inferior colliculus for analyzing FM signals. The returning echo also enters the inferior colliculus where it undergoes cross correlation with the stored replica of the sonar transmission. Neurons in the bat's auditory system are selectively sensitive to echo-like sounds (*2, 3*), and the cross-correlation operation probably involves such sensitivity. The existence of matched-filter properties as suggested by electrophysiological studies of the bat's

auditory brain is supported by the range-discrimination data.

At present this cross-correlation model is applicable to echo processing by bats that use short-duration, FM sonar cries. The model should prove useful in accounting for the well-known resistance of bats to confusion from multiple-target clutter interference and in explaining their remarkable proficiency at target identification, tracking, and interception (*6*). If the alternate expression for the correlation function, the power spectrum, is also available in the bat's brain, then the bat could distinguish many target characteristics from their echo signatures. Bats that use long-duration, constant-frequency signals with a short, terminal FM sweep (*Rhinolophus* and *Chilonycteris*, for example) may use cross-correlation processing on the last few milliseconds of their echoes.

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Infectious Goiter

The usual hypothesis given for the etiology of goiter in man is that the enlargement of the thyroid gland is a consequence of dietary iodine deficiency. Studies of iodine intake of goitrous and nongoitrous persons living in the same environment have not shown significant differences (1). The hypothesis that goiter is caused by, or is associated with, infection has not been rejected nor has it been adequately tested. Endemic goiter occurs, in general, among populations living in rural areas and belonging to lower socioeconomic groups. Several studies have shown that the drinking water of such populations is polluted with bacteria. Since shallow wells are more likely to be polluted than either deep wells or public water supplies we made the hypothesis that goiter is associated with drinking water obtained from shallow wells. In 1965 and 1966 we tested this hypothesis among people living in Richmond County in the tidewater area of Virginia. We found that there was an increased prevalance of goiter among persons from households supplied with water from shallow wells

compared with people who received their water from the public supply (2).

Now Werner *et al.* report that IgM levels are elevated in persons with goiter as compared with appropriate nongoitrous controls (3). It seems to us that, although other interpretations are also possible, these data provide additional support for the infectious hypothesis. Other tests of this hypothesis (which does not exclude the iodine hypothesis) are warranted.

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6 January 1971 ∎

Phenylthioacetate as a Stain for Cholinesterase

Booth and Metcalf (1) suggest the substitution of phenylthioacetate (PT) for acetylthiocholine (ATCh) as a histochemical stain for detection of cholinesterase. In the adult summer form but not the winter form of the female spider mite (*Tetranychus urticae*), PT was specific for the walls of the midgut and insensitive to $1 \times 10^{-7}M$ paraoxon; ATCh was specific for the synaptic area of the brain and the surface of nerves in formalin-fixed tissue (2). The cholinesterase sensitivity to paraoxon was found to vary in different strains of spider mites (3). Differences in histochemical staining of PT and ATCh can be expected among arthropods.

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Pesticide Concentration in Seawater

The assumption of Blanchard and Syzdek (1) that DDT might be concentrated in natural surface films of seawater should not be left to speculation for the readers of *Science*. Apparently these and other authors (2) are unaware that we have reported concentration factors of up to 10^5 for chlorinated pesticides in sea slicks (3). Their expectation that slicks would be areas of high biologic activity was similarly confirmed (3). It has been our express concern that this phenomenon may lead to much more rapid concentration of these toxicants in marine food chains than would be anticipated if dilution were homogeneous.

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